NeuroImage 169 (2018) 80–93

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

Domain-general and domain-specific neural changes underlying visual expertise

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A R T I C L E I N F O

Keywords:
Visual expertise
fMRI
Object recognition

A B S T R A C T

Visual expertise induces changes in neural processing for many different domains of expertise. However, it is unclear how expertise effects for different domains of expertise are related. In the present fMRI study, we combine large-scale univariate and multi-voxel analyses to contrast the expertise-related neural changes associated with two different domains of expertise, bird expertise (ornithology) and mineral expertise (mineralogy). Results indicated distributed expertise-related neural changes, with effects for both domains of expertise in high-level visual cortex and effects for bird expertise even extending to low-level visual regions and the frontal lobe. Importantly, a multivariate generalization analysis showed that effects in high-level visual cortex were specific to the domain of expertise. In contrast, the neural changes in the frontal lobe relating to expertise showed significant generalization, signaling the presence of domain-independent expertise effects. In conclusion, expertise is related to a combination of domain-specific and domain-general changes in neural processing.

Introduction

Experience and learning shape human behavior and influence the functional architecture of the brain. A widely studied exemplar of learning is visual expertise, defined as a superior performance in identifying and categorizing visually similar objects within a specific domain (Harel et al., 2013; Shen et al., 2014). Visual expertise has been associated with changes in the underlying neural activation for the expert object category, with evidence from many real-world domains of expertise as well as experimentally induced forms of expertise and learning in humans and primates (Gauthier et al., 1999; Sigala and Logothetis, 2002; Kourtzi et al., 2005; Sigman et al., 2005; Op de Beeck et al., 2006; Li et al., 2007; Wong et al., 2009; Folstein et al., 2013).

Despite the large body of available studies on this topic, a consensus has yet to be reached on the proper interpretation of their findings, as is demonstrated by the strongly differing conclusions in available literature reviews (e.g. McKone and Kanwisher, 2005; Curby and Gauthier, 2010; Harel et al., 2013). A recurring point of disagreement is the potentially important role played by specific brain areas, particularly the fusiform face-selective cortex (fusiform face area, FFA). Not surprisingly, many empirical studies have focused on this specific issue. Several fMRI studies in which experts were compared to novices have indeed demonstrated a relation between expertise and activation in the FFA in response to objects of expertise. These neural changes have been found in chess experts, car experts, plane experts, ornithologists and radiologists (Gauthier et al., 2000; Xu, 2005; Harley et al., 2009; Bilalić et al., 2011, 2014; McGugin et al., 2012a) as well as in participants who were extensively trained to recognize novel objects (e.g. “Greebles”, Gauthier et al., 1999; Behrmann et al., 2005). An EEG study also demonstrated a competition for neural resources between faces and objects of expertise in face-selective areas in OTC (Rossion et al., 2007). However, several other studies have failed to find an expertise effect in face-selective regions, including studies with real-world experts (Grill-Spector et al., 2004; Rhodes et al., 2004; Krawczyk et al., 2011) and laboratory-trained participants (Op de Beeck et al., 2006), even when using the original Greeble stimuli (Brants et al., 2011).

The presence of expertise-related activity has also been demonstrated in occipitotemporal cortex (OTC) beyond the FFA (Grill-Spector et al., 2004; Rhodes et al., 2004; Moore et al., 2006; Op de Beeck et al., 2006; Jiang et al., 2007; Wong et al., 2009; Harel et al., 2010; Brants et al., 2011; Krawczyk et al., 2011; Mongelli et al., 2016). Even areas outside the visual cortex have emerged in the search for expertise effects, including prefrontal and parietal regions (Moore et al., 2006; Harel et al., 2010; Krawczyk et al., 2011) and auditory association cortex for professional musicians (Hoenig et al., 2011).

All reviews agree that various forms of expertise exist and that

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https://doi.org/10.1016/j.neuroimage.2017.12.013
Received 16 July 2017; Accepted 5 December 2017
Available online 6 December 2017

expertise-related neural changes *might* depend upon stimulus characteristics and domain-specific task requirements (compare, for example, Richler and Gauthier (2014) and Harel et al. (2013)). In at least a subset of the studies for example, the increased response observed in the FFA may be due to the nature of the presented stimuli and the degree to which they resemble faces (Op de Beeck et al., 2006; Xu, 2005). However, there is surprisingly little direct evidence to support such claims. It remains unclear why the localization of expertise effects in visual cortex varies widely between studies, sometimes affecting the FFA and sometimes affecting other regions.

We aim to investigate the interaction between the specific domain of expertise and the localization and the extent of the underlying neural changes. To do this, we need to compare different domains of visual expertise and focus on the related patterns of activity in the entire visual cortex and even the brain at large. While some studies have already compared different domains of visual expertise (e.g. car experts vs bird experts: Gauthier et al., 2000; Xu, 2005; car experts vs plane experts: McGugin et al., 2012a), they only focused upon a limited set of ROIs and might therefore have missed potential expertise effects. Others adopted a broader perspective and performed at least some whole-brain univariate or multivariate analyses but were limited to only one domain of expertise (Harel et al., 2010; Bilalić et al., 2014; Mongelli et al., 2016). As a consequence, we lack insight into the degree of similarity (or disparity) between neural changes induced by different domains of visual expertise.

In the present fMRI study we combine large-scale univariate analyses, multi-voxel brain decoding and region-of-interest analyses to compare the changes in neural processing associated with two forms of expertise, bird expertise (ornithology) and mineral expertise (mineralogy). We have deliberately included one animate and one inanimate domain, because this seems to be the major distinction underlying the large-scale organization of neural object representations (e.g. Kriegeskorte et al., 2008; Mahon and Caramazza, 2009; Bracci and Op de Beeck, 2016). While mineralogy might seem an odd choice at first, minerals form a homogenous object category that is more representative of a nonliving category than for example the more commonly studied category of cars (Gauthier et al., 2000; Xu, 2005). Since cars are moving objects and the front views of cars resemble faces (Xu, 2005), they have often been depicted as living objects (e.g. the Pixar animation film series "Cars"). Comparing two very different domains of visual expertise offers us the opportunity to investigate whether expertise induces domain-specific neural changes, possibly showing a bias to affect those regions which are most activated by the object domain ("informative" regions; Op de Beeck and Baker, 2010; Brants et al., 2016). Alternatively, more general correlates of visual expertise that are similar across different domains could play a role, either at the level of specific regions of interest (Gauthier et al., 2000) or at a more distributed level (Harel et al., 2013). Importantly, to test these hypotheses we have to investigate patterns of activity not only at the level of individual areas, but more broadly across large cortical regions.

Material and methods

Participants

The study included 68 participants. Twenty-one candidate experts in ornithology, 27 candidate experts in mineralogy and 20 control participants took part in the behavioral session of this study. All participants completed perceptual and semantic measures for both domains of expertise (see details below). Based on the behavioral results, 10 candidate experts in mineralogy were excluded from further participation and analyses. One expert in ornithology was excluded for MRI safety reasons. The final sample of subjects consisted of 20 ornithologists (aged 26.4 ± 5 years, 5 females, average 8.6 years of experience (sd 4.6 years), apart from three outliers all within 3 and 10 years), 17 mineralogists (aged 25.3 ± 5 years, 7 females, average 6.4 years of experience (sd 3.7 years), apart from three outliers all within 3 and 8 years) and 20 control participants (aged 24.3 ± 3 years, 7 females, no experience with either birds or minerals). These sample sizes were larger than the number of participants included in the few other studies comparing two groups of experts (Gauthier et al., 2000; Xu, 2005). The subject groups were mostly matched for number of men/women. Previous research has indicated that men show an advantage for recognition of nonliving objects, while women tend to be better at recognizing living objects (McGugin et al., 2012b). While it would be interesting to investigate sex differences in these domains of expertise, our subject groups consisted of too few female experts to make the comparison. All ornithologists were active birdwatchers that had taken up this hobby out of interest. The group of mineralogists consisted in part of students with an academic degree in geology and in part of participants that actively collected and identified minerals. All participants were healthy adults with normal or corrected-to-normal vision and the three groups were matched for level of education. The study was approved by the Medical Ethical Committee of KU Leuven and all participants provided a written informed consent.

Behavioral session and determination of expertise level

All subjects participated in a behavioral session of approximately one hour, in which they carried out several computer and paper-and-pencil tasks. First, participants were asked to fill out a questionnaire in which their self-reported knowledge of birds and minerals was measured, as well as their general interest in classifying and determining objects. This questionnaire was a Dutch translation of the questionnaire used by Gauthier et al. (2014), in which the category-specific questions were attuned to birds and minerals. Second, all participants completed two perceptual discrimination tasks, one for each domain of expertise, to determine their level of expertise. Each discrimination task consisted of 80 pairs of colored images of either European bird species or of more or less well-known minerals, which were selected with the assistance of experts in both domains. The participants had to decide for each pair of images whether both images were of the same species in the case of birds or whether they shared the same chemical composition (polymorphs) in the case of minerals. Note that for both types of expertise, the discrimination task was not strictly (though largely) a perceptual task. Both visual (birds: shape and color of claws, beak, feathers, etc.; minerals: crystal structure) and non-visual (birds: birdsong, habitat; minerals: hardness) aspects play a role in the classification of birds and minerals. Furthermore, experts need domain-specific knowledge to know how to interpret the visual information (e.g., the fact that for some species of birds the male and female exemplars are very different). The pairs in both tasks (half 'same', half 'different') varied in difficulty. The images were presented sequentially: the first image appeared for 1 s, the second image remained on the screen until a same/different response was made by pressing one of two keys on the keyboard. The design of this discrimination task was inspired by tasks used in earlier fMRI studies of expertise (Gauthier et al., 2000; Gilaie-Dotan et al., 2012; Harel et al., 2010; McGugin et al., 2012a).

An additional semantic task was used to measure how well participants were able to name different objects of expertise, again for both domains of expertise. Participants were asked to name a list of 30 colored images as precise as possible, without being limited by a time constraint. Each answer was awarded one, two or three points, based on the specificity of the answer. For example, naming the correct bird species (and even giving the correct Latin name) would earn more points than naming the more general bird family. Participants with a knowledge of birds were considered bird experts if they reached an accuracy level of 65% on the bird discrimination task, which was the case for all candidate bird experts. Three participants who claimed to have no specific knowledge of birds reached the 65% boundary as well, however, they were not considered to be experts based on their low score on the semantic task for birds (maximal score of 15% correct, far below the average score of 65% for the included bird experts). For the selection of mineralogists the same logic was applied. However, the mineral discrimination task proved to be more difficult, therefore a threshold of 60% was applied. One candidate mineral expert did not reach the 60% threshold (score: 57.5%), but since his semantic score was very good (situated at the 76th percentile of semantic scores for all included mineral experts), he was still included in the study as a mineralogist. Ten other candidate mineralogy experts were excluded for further testing (no fMRI scan) because they did not reach the 60% discrimination threshold and did not compensate with a convincing score on the semantic task (scores situated below the 29th percentile of semantic scores for all included mineral experts). The thresholds for the discrimination tasks were chosen to make the distinction between experts and non-experts as clearly as possible, while taking into account the different characteristics of the performance on the two tasks. The selected thresholds for both tasks were significantly different from the chance level of 50%. Following the binomial distribution, the probability of answering exactly or more than 48 out of 80 trials (60%) correctly is $p = 0.046$, the probability of having exactly or more than 52 correct trials (65%) is $p = 0.0048$, under the null hypothesis of a distribution centered at 50%.

After the imaging data had been collected, we tested the participants' memory for the bird and mineral exemplars that had been presented to them during the scans (see fMRI procedure and experimental design). In this delayed recognition task, for both categories the 20 original images were interspersed with 20 distracters and participants were asked to indicate which of these images they had or had not seen during the experiment.

Finally, we assessed the participants' recognition ability in a third, neutral domain to assess whether the experts' performance on the relevant discrimination task (e.g. bird task for ornithologists) was related to a more domain-general skill of fine object recognition. Although participants' performance on the discrimination task of the "opposite" domain (e.g. mineral task for ornithologists) already served as a baseline measure (since it concerns an object category of which participants have no specific knowledge), we also administered the Cambridge Face Memory Test (CFMT, Duchaine and Nakayama, 2006) to all participants.

Apparatus

Imaging data were collected using a 3T Philips Ingenia CX scanner with a 32-channel head coil at the Department of Radiology of the University Hospitals Leuven. Functional images were acquired via an EPI sequence with a TR of 3 s, TE of 30 ms, 54 slices, 2.5×2.56 mm in plane voxel size, slice thickness of 2.5 mm, inter-slice gap of 0.2 mm, flip angle of 90° and an 84×82 acquisition matrix, covering the whole cerebral cortex. We collected a high-resolution T1-weighted anatomical image for each participant (182 slices, $0.98 \times 0.98 \times 1.2$ mm resolution, TR = 9.6 ms, TE = 4.6 ms, 256×256 acquisition matrix). The stimuli were presented using PsychToolbox 3 (Brainard, 1997) in Matlab and projected onto a screen which could be viewed through a mirror mounted on the head coil.

fMRI procedure and experimental design

Imaging data were collected in a block-design experiment consisting of 10 runs, each lasting 255 s. Within each run, 7 categories of stimuli were presented: birds, minerals, faces, scenes, living objects (animals), nonliving objects and scrambled images (see Fig. 1). Each category contained 20 gray-scale images. The images were presented on a uniform gray background at a uniform size of 300×300 pixels in a random left or right orientation and with a small position jitter (maximum 50 pixels in horizontal and vertical direction) around the fixation point. The order in which the categories were presented was balanced over runs and participants and the stimulus order within each category block was randomized. Each block contained 20 stimulus trials, of which three trials were an immediate repetition of the previously presented image but with a random position and orientation. Participants were asked to press a button to signal these successive image repetitions regardless of position and orientation changes. Responses were collected via a response box.

Analyses

fMRI preprocessing and statistical analysis

All imaging data were preprocessed using the Statistical Parametric Mapping software package (SPM12, Welcome Department of Cognitive Neurology, London). Functional images were corrected for slice timing differences as well as head movements by realignment to the mean image. The images were smoothed using a Gaussian kernel of 8 mm full-width at half maximum (FWHM) for univariate second level analyses, and a Gaussian kernel of 5 mm FWHM for the univariate ROI analyses and for all multi-voxel analyses (subject classification, generalization and representational similarity analyses). Both anatomical and functional images were normalized to the standard Montreal Neurological 152-brain average template and the voxels were resampled to a voxel size of $2.5 \times 2.5 \times 2.5$ mm. Due to some technical difficulties and excessive head motion, a number of functional runs had to be excluded from further analyses. We controlled for excessive head motion during scanning by discarding all runs in which participants moved more than half a voxel size (1.25 mm) on two consecutive images. For 41 participants (14 ornithologists, 11 mineralogists and 16 controls), we were able to include all 10 functional runs. For 10 participants (4 ornithologists, 4 mineralogists and 2 controls) 9 runs were included, for 4 participants (2 ornithologists and 2 controls) we included 8 runs and for the remaining 2 participants (mineralogists) we included 7 runs. For each participant a general linear model (GLM) was fitted to estimate the linear relationship between the experimental conditions and the recorded neural activation in each voxel. The fixation condition was not explicitly modeled. Motion realignment parameters were added as regressors to control for signal variation due to head motion. Further analyses were performed using t-tests between coefficients of different experimental conditions.

Regions of interest

Given that object recognition has been shown to be sustained by a neural system encompassing low- and high-level regions in ventral visual cortex as well as frontal regions (e.g. Fenske et al. (2006)), we delineated three large but mutually exclusive anatomically defined regions of interest (aROIs). First, we selected all voxels that were significantly active above the threshold of $p < 0.001$ (uncorrected) in the contrast [all conditions - fixation]. Anatomical masks, created by using the WFU PickAtlas Toolbox (Wake Forrest University PickAtlas, fmri.wfubmc.edu/cms/software), were used to define the following bilateral aROIs (Fig. 2): a low-level visual aROI (Brodmann areas 17 and 18, which included V1 and nearby cortical regions, defined in all 57 subjects), a high-level visual aROI (Brodmann areas 36, 37 and 20, defined in all 57 subjects) and the complete frontal lobe (including motor cortex, defined in all 57 subjects). Given that these masks provide a thin cortical thickness which is not realistic given the smoothed nature of our fMRI data for the between-group comparisons, the anatomical masks were expanded by two voxels in all directions to make sure that most relevant active voxels were included. The resulting minor overlap between the low-level visual aROI and the high-level visual aROI was removed from both resulting masks. Seven additional functional ROIs (fROI) were delineated manually in each individual participant, independent from the experimental data. These fROIs, that were defined using different functional contrasts, all included spatially contiguous voxels that exceeded the uncorrected statistical threshold of $p < 0.0001$. Significantly active voxels were displayed on coronal slices and manually selected. Only clusters consisting of a minimum of 20 voxels were selected. When less than 20 active voxels were found, a more liberal uncorrected threshold of $p < 0.005$ was applied. Here again, the minimum cluster size was taken into account, and the fROI was not defined if cluster size was smaller than 20 voxels. The fusiform face area (left FFA: 54 subjects; right FFA: 56 subjects) and the occipital face area (OFA) were defined by the contrast [faces - nonliving] in combination with anatomical criteria. Due to the

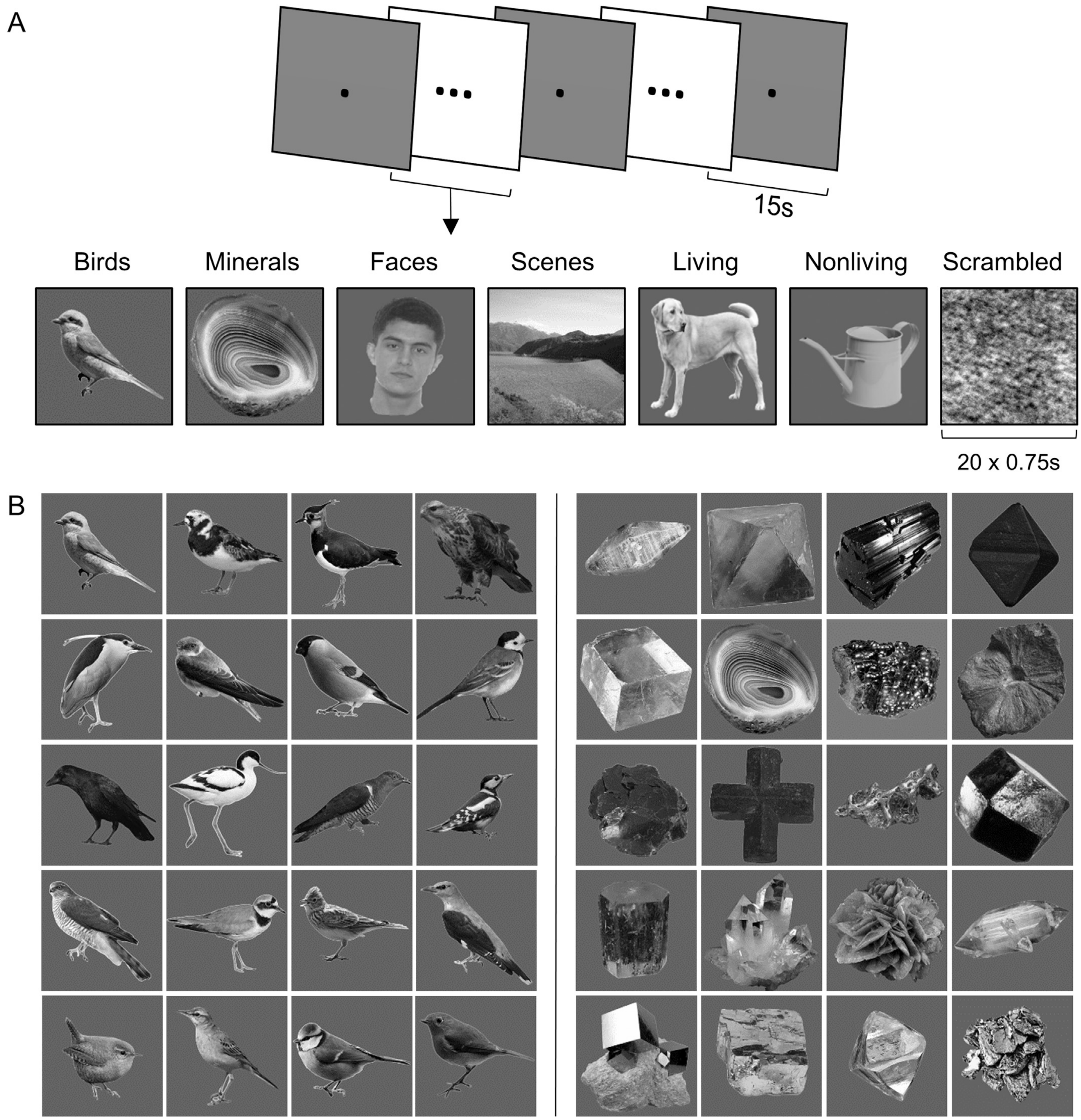

Fig. 1. (A) Schematic overview of the design of one experimental run. Images of 7 categories were presented in a block-design (20 grayscale images per block). At the start, in the middle and at the end of each run a fixation block of 15s was presented. (B) The 20 bird stimuli and 20 mineral stimuli that were used during the experiment.

fact that OFA could only be selected in a limited number of participants (38 left and 44 right), this region was left out of any further analyses. For the selection of the parahippocampal place area (PPA; left PPA: 57 subjects; right PPA: 57 subjects), voxels around the parahippocampal gyrus that showed responsiveness for the contrast [scenes - nonliving] were delineated. We defined two parts of lateral occipital complex (LOC) using the [nonliving – scrambled] contrast: a more posterior part in lateral occipitotemporal cortex (pLOC; left pLOC: 57 subjects; right pLOC: 57 subjects) and a more anterior part in ventral occipitotemporal cortex (aLOC; left aLOC: 57 subjects; right aLOC: 57 subjects). Both regions were selected in a mutually exclusive way. Finally, a region selective for living objects (left Living: 57 subjects; right Living: 56 subjects) and a region selective for nonliving objects (left Nonliving: 56 subjects; right Nonliving: 56 subjects) were delineated using the contrasts [living - nonliving] and [nonliving - living] respectively. Analyses in both the anatomical and the functional ROIs were performed across hemispheres (see e.g. Harel et al., 2010). The average sizes and MNI coordinates of all the ROIs mentioned above are presented in supplementary material (section A, Table S1).

Univariate fMRI analyses

We performed conventional univariate fMRI analyses to determine

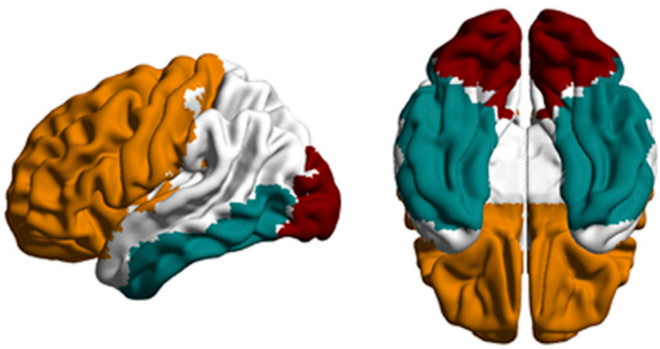

Fig. 2. Lateral and ventral view of the three anatomically defined aROIs. The low-level visual aROI is indicated in dark red, the high-level visual aROI in dark green and the frontal lobe in orange. The masks were visualized using BrainNet Viewer ((Xia et al., 2013) http://www.nitrc.org/projects/bnv/) and custom Matlab code.

the presence of heightened neural activation in experts compared to novices in response to objects of expertise. We calculated the mean response per voxel elicited by the different experimental conditions and compared these mean activations (beta values) between subject groups. This way, we performed whole-brain second-level analyses as well as group comparisons within specific ROIs. The effect of expertise for birds was defined by the contrast [birds – base] in which the "base" condition was a combination of the living and nonliving condition. The contrast [minerals - base] was used to define the expertise effect for minerals. For all univariate analyses, we first applied a stringent threshold of $p < 0.05$ corrected for family-wise error. However, when no effects survived, we lowered the threshold to $p < 0.0001$ (uncorrected, minimum cluster size of 10 voxels, see Lieberman and Cunningham (2009)) for all bird expertise analyses and an uncorrected threshold of $p < 0.001$ (minimum cluster size of 10 voxels) for the mineral expertise analyses. Note that these univariate maps are not meant to demonstrate significance for individual voxels, but instead to visualize where the voxels with the clearest univariate differences and thus with potential relevance for the classifiers tend to be.

Multivariate fMRI analyses: subject classification

With this analysis, we tried to answer the following question: can we make a distinction between subject groups based on their neural response patterns for a specific condition? These subject classification analyses were applied in each ROI to discriminate ornithologists from control participants and mineralogists from control participants (see Fig. 3A). The response per voxel per subject was defined by the univariate contrast of one of the expertise conditions versus base, e.g. [birds – base]. The contrast values were standardized by subtracting the mean value across all voxels in the subject-specific response pattern and dividing this result by the standard deviation across voxels. A linear support vector machine (SVM) was applied using the libsvm Matlab toolbox (Chang and Lin, 2011) with similar parameters as Bulthé and colleagues did (Bulthé et al., 2015). To train and test the SVM model, we used a leave-pair-out cross-validation (LPOCV) technique, as was used by Ung et al. (2014). For each of the two subject groups, a participant was randomly selected and left out of the training sample. Next, the classifier was trained on all subjects except for the left-out pair, which was subsequently used to test the trained model. Since all subjects viewed the same images for all the object categories, the training and testing of the classifier happened on

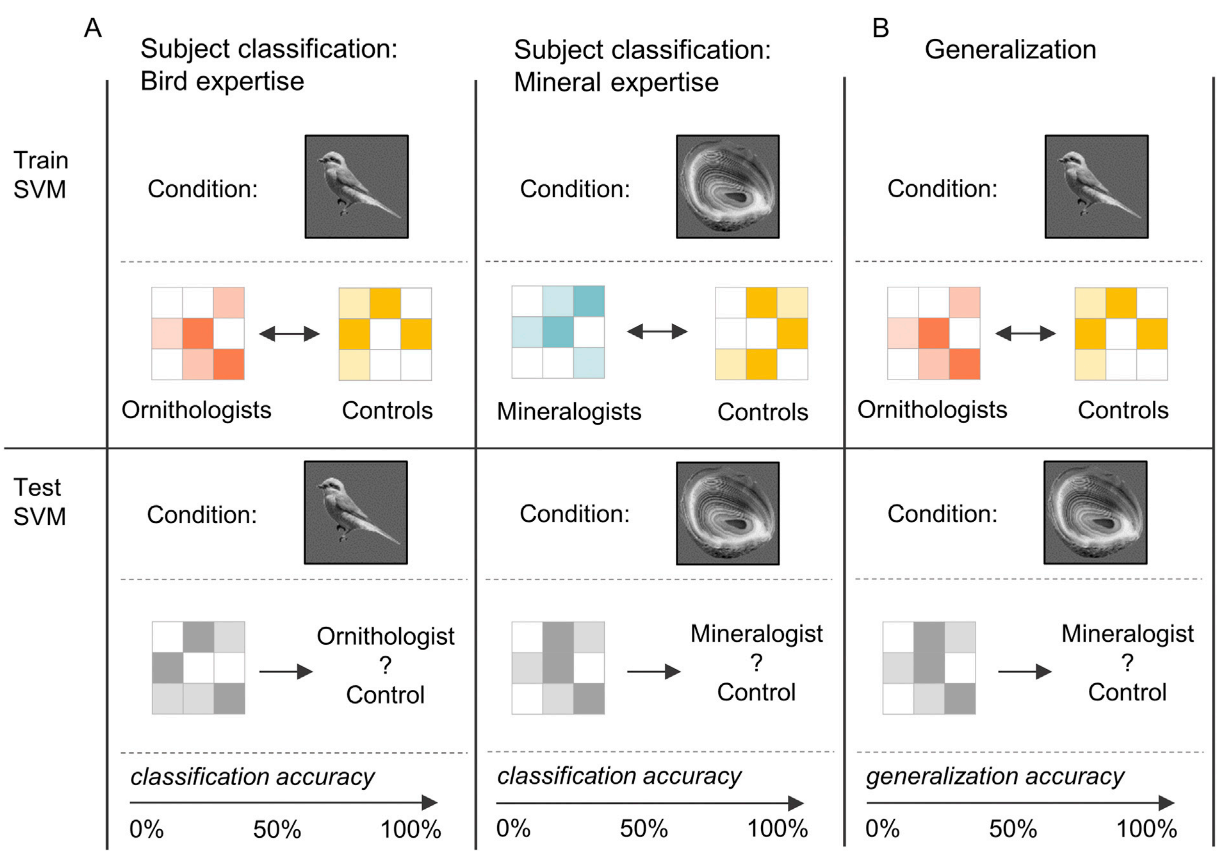

Fig. 3. (A) Schematic overview of the subject classification analyses for bird expertise and mineral expertise. A classifier was trained to make a distinction between the expert group and the control group based on their neural responses for the expert object condition (birds or minerals). Subsequent testing resulted in a classification accuracy. (B) Schematic overview of the generalization analysis. A classifier was trained on the expertise effect for one domain of expertise (e.g. bird expertise: the distinction between ornithologists and control participants for the category of birds) and tested on the other domain of expertise (e.g. mineral expertise: the distinction between mineralogists and control participants for the category of minerals). The generalization analysis was performed in two directions.

identical images. This procedure was repeated until each participant was left out once. In the case of unequal group sizes, the procedure was repeated until each participant of the smallest group was left out once. The decoding accuracy was calculated as the proportion of times in which test participants were correctly classified as belonging to one of the two subject groups. To control for slight differences in decoding accuracies due to the random selection (pairing) of test data, the LPOCV technique was iterated 1000 times and the decoding accuracies were averaged across all iterations. The higher this resulting decoding accuracy, the better the classifier was able to make a distinction between the two groups. In order to determine the significance threshold for the decoding accuracies, we applied Monte Carlo permutation tests (Mourão-Miranda et al., 2005). The above described LPOCV technique was again repeated 1000 times, only this time the class labels of the training sample were randomly shuffled before the model was trained, leading to a distribution of decoding accuracies based on random information. A 95% confidence interval around the mean of this distribution was calculated to determine the significance threshold for each comparison. As a sanity check, we checked that the significance thresholds obtained through permutations were very similar and not more liberal compared to the threshold expected from a simple (parametric) binomial test. According to such a binomial test, results above 62.5% would be significant with a total of 40 participants, as in classifications involving ornithologists and controls. For mineralogists and controls (N = 37), the parametric threshold would be 62.2%.

Furthermore, for each individual participant a mean decoding accuracy was calculated by dividing the number of times this participant was classified as an expert by the number of times the data of this participant were used as test data. This was done for the two comparisons mentioned above: we calculated the proportion of times ornithologists and control participants were classified as an ornithologist and the proportion of times mineralogists and control participants were classified as a mineralogist. These "proportions decoded as expert" were then related to the different behavioral measures of expertise (results in Table 1).

Multivariate fMRI analyses: generalization

To check whether potential differences in neural representations between control participants and bird experts were similar to the differences in representations between control participants and the group of mineral experts (and vice versa), we tested generalization of subject classification (Fig. 3B). In particular, we tested whether the classifier that was trained to make a distinction between the control group and one expert group based on the objects of expertise of that expert group (e.g., birds for ornithologists), was also able to make a distinction between the control group and the other expert group using their objects of expertise (e.g., minerals for mineralogists). Within each ROI, generalization was tested in both directions: training the classifier on the distinction ornithologists vs. control participants and testing on mineralogists vs. control participants, and vice versa. The overall "generalization accuracy" was calculated by averaging the decoding accuracies for both directions. To determine the significance threshold, we applied for each direction of generalization the same random permutation method as described above. This resulted in two distributions of decoding accuracies based on random information. By randomly selecting half of the decoding accuracies from each distribution and combining these selected values, we created a new distribution that was used to determine the significance threshold for the generalization accuracy. Again, the obtained thresholds were similar to the thresholds which would be observed using a parametric binomial test with the number of participants involved (N = 57). Hence we used a parametric method to calculate the 95% confidence interval around the proportion of subject generalization in order to compare it to the maximal generalization (see next paragraph).

Maximal generalization: simulations

We have already shown previously through simulations how the amount of generalization is limited by the classification accuracy in the two datasets between which the generalization is tested (Brants et al., 2016). If the two datasets differ in classification accuracy, then the generalization accuracy will be somewhere in between. We implemented these simulations with the classification accuracies obtained in the current dataset in order to quantify the maximally expected generalization accuracy given the empirically measured classification accuracies. A detailed explanation of this simulation approach is given in Brants et al. (2016).

Multi-voxel representational similarity analyses

Within the high-level visual aROI, multi-voxel patterns of activation for all the seven different conditions were correlated in a pairwise manner as a measure of their similarity or distinctness. As a first step, the data set for each participant was randomly divided into two equally sized subsets of runs (one half of the data amounted to 4 or 5 runs in which each condition was presented twice). Beta values for each voxel of the high-level visual aROI were standardized by subtracting the mean value across all conditions. For each participant, the activation patterns of all conditions in the first subset of runs were correlated with the second subset. This procedure of dividing the data and computing the correlations was repeated 100 times, resulting for each participant in a matrix of correlations averaged across those repetitions. The individual similarity matrices were averaged across participants within each group. The resulting group similarity matrices, in which each cell contained the correlation between two specific conditions, were visualized using multidimensional scaling (MDS), which arranged the experimental conditions in a two-dimensional space according to similarity in activation patterns. Highly correlated conditions are shown closer together whereas less correlated conditions are located further apart in the MDS plots. This method allowed us to investigate potential differences between experts

Table 1
Correlations between the "proportion decoded as expert" and performances on two behavioral tasks.

		Low-level visual		High-level visual		Frontal lobe	
Classification	Behavioral task	r	p	r	p	r	p
Ornithologists and controls: classified as ornithologists	Discrimination birds	0.544	0.0003	0.787	< 0.0001	0.628	< 0.0001
	Semantic birds	0.579	< 0.0001	0.812	< 0.0001	0.677	< 0.0001
Mineralogists and controls: classified as mineralogists	Discrimination minerals	-0.057	0.738	0.442	0.006	0.258	0.123
	Semantic minerals	-0.080	0.680	0.267	0.055	0.162	0.170

The "proportion decoded as expert" represent the proportion of times a subject was either classified as being an ornithologist (ornithologists and control participants, N = 40) or as a mineralogist (mineralogists and control participants, N = 37). The four aROI x classification situations in which the subject classification was significant, are indicated by a bold frame.

and novices in the representational similarity between the categories of stimuli.

Results

Behavioral indices of expertise

The final sample included 57 participants from three groups: ornithologists (N = 20), mineralogists (N = 17), and control participants (N = 20). A variety of behavioral indices showcased the domain-specific expertise of participants. Fig. 4 displays the proportion correct scored by the three subject groups on the discrimination and semantic tasks for birds and minerals, these scores were used to select the experts. For the discrimination tasks, we calculated d' (d-prime) for each participant based on the number of Hits (subject correctly responds that birds/minerals are the same) and False Alarms (subject responds that birds/minerals are the same while in reality they are different; $d' = z(H) - z(FA)$). These d' values were used in the following analyses. On the bird discrimination task, the ornithologists scored significantly higher than the mineralogists ($t(35) = 8.39$, $p < 0.0001$) and the control participants ($t(38) = 9.71$, $p < 0.0001$). The mineralogists outperformed the ornithologists ($t(35) = 7.50$, $p < 0.0001$) and the control participants ($t(35) = 7.84$, $p < 0.0001$) on the mineral discrimination task.

The mineralogists' performance on the mineral discrimination task was significantly lower than the ornithologists' score on the bird discrimination task ($t(35) = 5.67$, $p < 0.0001$). However, it should be noted that the two discrimination tasks were not calibrated and are therefore not really comparable. It might very well be that the mineral discrimination task was more difficult. This can be illustrated by a linear regression analysis showing that an ornithologist with 7 years of experience would reach a d' of 2.23, while an equally experienced mineralogist would only get a d' of 0.91 on the mineral discrimination task. Note that the control participants showed no difference in performance between the bird discrimination task and the mineral discrimination task ($t(19) = 1.35$, $p = 0.19$), for both tasks they performed around chance level.

The semantic tasks showed the same pattern of results. On the semantic task for birds, the ornithologists' score was higher than the mineralogists' ($t(19.95) = 13.23$, $p < 0.0001$), which was in its turn higher than the score of the control participants ($t(35) = 2.50$, $p = 0.015$). On the semantic task for minerals, the mineralogists outperformed the ornithologists ($t(23.87) = 9.79$, $p < 0.0001$) and the control participants ($t(18.33) = 11.26$, $p < 0.0001$).

Finally, ornithologists with more years of experience tended to score better on the bird expertise tasks compared to less experienced ornithologists. Self-reported years of experience with birds was significantly correlated with performance on the semantic task for birds (Pearson's $r = 0.46$, $p = 0.02$) and the relation to the performance on the discrimination task also tended to be positive, although not significant (Pearson's $r = 0.42$, $p = 0.06$). For mineralogists, there was no significant correlation between years of experience and the scores on the mineral tasks (semantic task: Pearson's $r = 0.31$, $p = 0.11$; discrimination task: Pearson's $r = 0.40$, $p = 0.11$). We did not find a correlation between the age of the experts and their scores on the discrimination or semantic tasks for their expert object category (Orn.: discrimination task: Pearson's $r = 0.01$, $p = 0.95$; semantic task: Pearson's $r = 0.21$, $p = 0.38$; Min.: discrimination task: Pearson's $r = -0.05$, $p = 0.86$; semantic task: Pearson's $r = 0.41$, $p = 0.10$).

As was mentioned in the methods section, the discrimination tasks and the semantic tasks were used to select the experts. Therefore, the group differences on these tasks are to be expected and circular. However, other behavioral measures showed clear differences between the three subject groups as well. On the expertise questionnaire, apart from their number of years of experience, participants also indicated on a scale of 1–9 how often they read text about birds/minerals and how often they looked at images of birds/minerals. The responses clearly showed a difference between the three subject groups, with the experts spending more time with their specific domain of expertise and the control participants not really spending time on either domain (text birds: Orn.: 8.0, Min.: 2.2, Con.: 1.7; images birds: Orn.: 8.0, Min.: 3.6, Con.: 2.0; text minerals: Orn.: 1.7, Min.: 7.2, Con.: 1.4; images minerals: Orn.: 1.6, Min.: 6.9, Con.: 1.6).

Furthermore, on the one-back task participants performed while in the scanner, both expert groups achieved higher scores when the task involved images belonging to their domain of expertise compared to images belonging to the other expert domain. For each participant and for each condition we calculated d' (d' for condition Birds: Orn.: 2.88, Min.: 1.89, Con.: 2.21; d' for condition Minerals: Orn.: 2.75, Min.: 2.55, Con.: 2.38). A two-way repeated measures ANOVA with subject group as a between-subjects factor and condition (7 levels) as a within-subjects factor revealed a significant interaction ($F(12,324) = 2.98$, $p = 0.001$) between subject group and stimulus condition, accompanied by a significant main effect of stimulus condition ($F(6,324) = 41.77$, $p < 0.0001$) but no main effect of subject group ($F(2,54) = 2.03$, $p = 0.142$). The interaction between stimulus condition and subject group was also significant when restricted to birds and minerals ($F(2,54) = 10.76$, $p < 0.0001$). To estimate the increase in discriminability both expert groups showed for their expert condition compared to the remaining conditions, we calculated d'(expert condition) – d'(remaining conditions). The increase in discriminability did not differ between the two expert groups ($t(35) = 1.49$, $p = 0.15$).

The findings were similar for the delayed recognition task in which participants indicated which bird and mineral images they had or had not seen during the scans. Again, for each participant and for each condition d' was calculated. A two-way repeated measures ANOVA for unbalanced groups with subject group as a between-subjects factor and condition (birds or minerals) as a within-subjects factor showed that both expert groups were better able to recognize presented and not-presented images from their specific domain of expertise (significant interaction: $F(2,54) = 52.59$, $p < 0.0001$; d' for condition Birds: Orn.: 3.14, Min.: 1.16, Con.: 1.09; d' for condition Minerals: Orn.: 2.40, Min.: 2.61, Con.: 2.15). The increase in discriminability (d'(expert condition) – d'(nonexpert condition)) for the delayed recognition task was

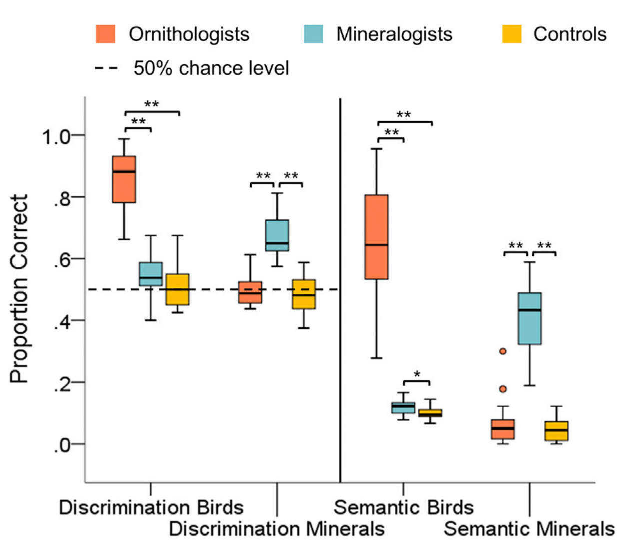

Fig. 4. Results for the behavioral expertise tasks (discrimination and semantic tasks) for ornithologists (N = 20), mineralogists (N = 17) and control participants (N = 20). Boxplots display the median proportion correct and interquartile range, whiskers indicate the minimum and maximum values and dots represent outliers (>1.5 x interquartile range). Unpaired t tests were used to determine significance, which is indicated by * ($p < 0.05$) or by ** ($p < 0.0001$). For the discrimination tasks (left panel), chance level performance was at 50%. The expert group always outperformed the other two groups on those tasks related to their field of expertise. These scores were used to select the experts (see 2.2. Behavioral session and determination of expertise level).

significantly different between the two expert groups ($t(35) = 3.10$, $p = 0.004$), mineralogists showed an advantage over ornithologists.

Finally, we tested whether there was any relationship between the participants' performance on the expertise-related tasks and the third neutral domain of face perception as measured by the CFMT. The three subject groups did not differ in their face recognition ability ($F(2,54) = 0.37$, $p = 0.69$; Orn.: 75% correct, sd = 12.9%, Min.: 74% correct, sd = 10.8%, Con.: 77% correct, sd = 14.5%). For neither of the two expert groups a significant correlation could be found between the experts' performance on the CFMT and their performances on the expertise tasks for their domain of expertise (Orn.: discrimination task: Pearson's $r = -0.23$, $p = 0.33$; semantic task: Pearson's $r = -0.17$, $p = 0.47$; Min.: discrimination task: Pearson's $r = 0.26$, $p = 0.31$; semantic task: Pearson's $r = 0.32$, $p = 0.21$).

Expertise-related multi-voxel patterns of selectivity

The fMRI scans probed the patterns of activity related to stimuli from the two domains of expertise, birds and minerals, as well as five other reference conditions: faces, scenes, living objects, nonliving objects and scrambled images (Fig. 1).

We searched for expertise-related changes in the multi-voxel patterns by means of subject classification methods, following the scheme in Fig. 3A. If the neural response patterns to a particular stimulus condition would be altered by expertise, then we should be able to reliably classify subjects as belonging to a particular subject group based upon these patterns. Three large aROIs were anatomically defined: a low-level visual aROI, a high-level ventral visual aROI, and the frontal lobe. The classification of subjects was tested for two selectivity patterns: the selectivity for birds and selectivity for minerals. Two group comparisons were made: (1) ornithologists vs. control participants and (2) mineralogists vs. control participants.

As shown in Fig. 5A, the multi-voxel pattern classification was able to make a distinction between ornithologists and control participants based on the selectivity for birds in each aROI. Classification accuracies in the different aROIs ranged from 76.9% ($p < 0.0001$) to 91.3% ($p < 0.0001$). A very different result was found for mineral expertise (Fig. 5B). The distinction between mineralogists and control participants could only be made based on neural response patterns in high-level visual cortex (67.4%, $p = 0.024$). No significant classification was found in the low-level visual aROI (53.2%, $p = 0.301$) nor in the frontal lobe (61.3%, $p = 0.117$).

Although high-level visual cortex showed significant effects for each expertise domain, there was an obvious difference in effect size between domains (subject classification accuracies: 91.3% for bird expertise, 67.4% for mineral expertise). We hypothesized that this difference in effect size might be explained by a difference in the level of expertise between ornithologists and mineralogists. To address this issue, we performed the same analysis on a subset of the expert groups that were matched for their level of expertise. Because the discrimination and semantic tasks were not comparable between the two domains of expertise (see above), we calculated a new measure of experience using the participants' answers on the expertise questionnaire. For each expert, we calculated an average score indicating how often they read text about and looked at images of their objects of expertise (see above) and multiplied this with the number of years of experience they had. On average, the group of ornithologists had more "active experience" than the group of mineralogists (Orn.: 68.2, Min.: 43.9; $t(35) = 2.35$, $p = 0.025$). To match the two expert groups on this measure of experience, we temporarily excluded the 7 ornithologists with the most experience and the 4 mineralogists with the least experience, resulting in two groups with 13 experts each that did not differ on their level of experience (Orn.: 47.9, Min.: 50; $t(24) = 0.22$, $p = 0.83$). The subject classification accuracies in the high-level visual aROI for the matched groups were very similar to the ones that were obtained for the complete expert groups. The 13 least experienced ornithologists could be distinguished from the control participants equally well as when the most experienced ornithologists were included (90.1% vs. 91.3%). The same was true for the group of mineralogists when only the 13 most experienced participants were included (67.2% vs. 67.4%). These results showed that the difference in decoding accuracies in high-level visual cortex between the two domains of expertise was not influenced by the difference in level of experience

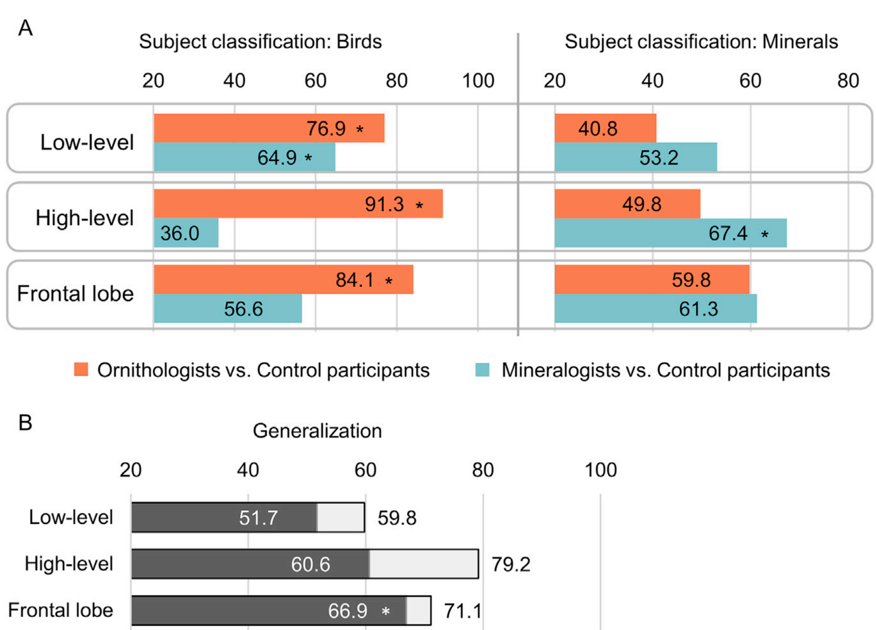

Fig. 5. (A) Results for the subject classification analyses in percentages. Monte Carlo permutation tests were used to determine the significance threshold for each classification accuracy (see Materials and Methods), significance is indicated by a *. The left panel shows the classification of participant groups based on their neural response patterns for birds. The classifier was able to make a distinction between ornithologists and control participants in all three aROIs. The right panel shows the classification for the category of minerals, with a significant distinction between mineralogists and control participants in the high-level visual aROI. (B) Results for the generalization analysis. Generalization accuracies are depicted by the dark grey bars, the light grey bars show the maximal generalization that could be expected given the classification performances for the two expertise effects in each specific aROI (see Materials and Methods). Significance is indicated by an asterisk.

between the two groups. (Remark: the analyses mentioned below were performed on the complete expert groups.)

As far as significant classification was possible for objects of expertise, that is, in all aROIs for ornithology and in high-level visual cortex for mineralogy, this classification was in each case higher than the classification obtained when the other group of experts was classified based upon neural activity patterns associated with the same objects (Fig. 5). Ornithologists could not be distinguished from controls based upon the minerals condition. Likewise, mineralogists and controls could not be differentiated based on the birds condition in high-level visual cortex. Curiously, this same differentiation was possible in low-level visual cortex (64.9%, $p = 0.032$), albeit to a lesser extent than for ornithologists.

Overall, these findings fit with the general prediction that developing expertise alters the processing of objects in the domain of expertise. The findings are further confirmed by correlational analyses. We analyzed the "proportion decoded as expert" of each participant, to gain a better understanding of which participants were most often classified as being either an ornithologist (vs. a control participant, based on their neural response patterns for birds) or a mineralogist (vs. a control participant, based on their neural response patterns for minerals). We correlated the proportion of times participants (ornithologists and control participants) were classified as being an ornithologist ("proportion decoded as expert"), with their behavioral scores on the bird discrimination task (d') and the semantic task for birds. The same correlations were calculated for participants classified as being a mineralogist (mineralogists and control participants), using the scores on the mineral expertise tasks. Results can be found in Table 1. Furthermore, in Fig. S2 in the supplementary material, scatterplots display the relation between the participants' scores on the discrimination tasks and the semantic tasks on the one hand and the "proportion decoded as expert" in the high-level visual aROI on the other hand.

For the comparison between ornithologists and control participants, in all three aROIs there was a significant positive correlation between the proportion of times participants were classified as ornithologist and the scores on the discrimination task and semantic task for birds. The higher a participant's scores on the bird expertise tasks, the more likely this participants was to be taken for an ornithologist by a model that was trained to make the distinction between ornithologists and control participants based on their neural representations for birds. In the high level visual aROI, we also found a significant positive correlation between the proportion of times participants were classified as being a mineralogist and the scores on the mineral discrimination task. The correlation with the scores on the semantic task for minerals tended to be positive as well.

Domain-specific and domain-general signatures of expertise

The rationale of our design with multiple types of expertise was to investigate whether effects of expertise are similar across different domains. Is bird processing in ornithologists changed in a similar way as mineral processing in mineralogists? To answer this question, we tested whether subject classification could be generalized across domains of expertise. More specifically, we tested whether a classifier that was trained to make a distinction between ornithologists and control participants based on their response patterns for birds, generalizes to the distinction between *mineralogists* and control participants based on their response patterns for *minerals*, and vice versa (see Fig. 3B). This generalization was tested in both directions in all three anatomical ROIs and an average accuracy was calculated for each aROI. The lower the generalization accuracy compared to the classification accuracies, the more evidence for domain specificity of expertise effects. The higher the generalization accuracy, the more evidence for domain-general representations.

Aside from the generalization performance, we calculated the maximal generalization that could be expected (see Materials and Methods & Brants et al., 2016). This maximal generalization, which is in between the classification performances shown in Fig. 5, is important as a benchmark. First, if it is low, which is a consequence of low decoding performance, then the generalization analysis has insufficient sensitivity to differentiate between domain-specific and domain-general representations. More specifically, we have insufficient sensitivity when the maximum generalization is lower than our threshold of significance (61.8%–64.7%). This was the case for the low-level visual aROI. Thus, in this region the signatures of expertise in the two domains were not strong enough to interpret the outcome of the generalization analysis.

In the high-level visual aROI, the theoretical maximal generalization was 79.2%, well above the threshold of significance. However, in the empirical data there was no significant generalization, with the generalization accuracy at 60.6%. Given that the 95%-confidence interval around a proportion of 0.606 with $N = 57$ is [0.479 0.733], this subject generalization was significantly lower than the maximum generalization of 79.2%. Thus, at least part of the expertise effects on the neural representations of birds and minerals in high-level visual cortex were domain-specific. The way in which neural processing of expert objects in high-level visual cortex was changed by expertise depended upon the domain of expertise.

In the frontal lobe we found a different result. Generalization accuracy was significant at 66.9%, close to the predicted maximal generalization performance of 71.1%. This significant generalization signaled a substantial "overlap" between the two expertise effects in these regions. The result in the frontal lobe was remarkable, since we could not find a significant subject classification for mineralogists compared to control participants in this region. The fact that the generalization in this aROI did work, suggested that, although the decoding accuracy in the frontal lobe failed to reach significance for one of the two datasets, there must still be some meaningful information present that points to a distinction between mineralogists and control participants (similar findings in earlier studies: Oosterhof et al., 2012; Brants et al., 2016).

Taken together, the generalization of subject classification classifiers across domains of expertise indicated that expertise-related neural changes tend to reflect domain-specific effects in high-level visual cortex, whereas more general domain-independent effects of expertise were found in the frontal lobe.

Univariate effects of expertise

In the previous analyses, multi-voxel pattern analysis (MVPA) results showed the presence of expertise effects for both bird expertise and mineral expertise. Because MVPA does not give a direct indication of which voxels or sub-regions drive classification, the next logical step is to examine the more fine-grained locations of these expertise effects. The simplest approach is to perform a univariate test of the voxel-wise contrast value which was used in the classification. Starting with bird expertise, we compared the brain activation for the [birds-base] contrast in bird experts with the same contrast for all bird novices (mineral experts and control participants). Analyses revealed a large bilateral cluster in lateral ventral temporal cortex that was significantly more active for bird experts compared to novices (Fig. 6A). MNI coordinates for the peak voxels in left and right hemisphere were (−51, −57, −20) and (37, −55, 20) respectively. Furthermore, some more scattered effects could be found in left prefrontal cortex. The latter effects disappeared when the threshold was increased to $p < 0.05$ corrected for family-wise error. When comparing bird experts to the group of control participants in itself, the distribution of effects was largely the same.

Ventral temporal cortex is known to house a complex functional organization. Fig. 6C shows a ventral cortical view of the bird expertise effect and the mineral expertise effect in combination with outlines of the most relevant empirically measured regions with a functional preference for living objects, nonliving objects, as well as the fusiform face area. The spatial distribution of the bird expertise effect does not align with any of these functional divisions.

In addition, we quantified the bird expertise effects in 6 bilateral fROIs (FFA, PPA, pLOC, aLOC, a Living and a Nonliving region) that were

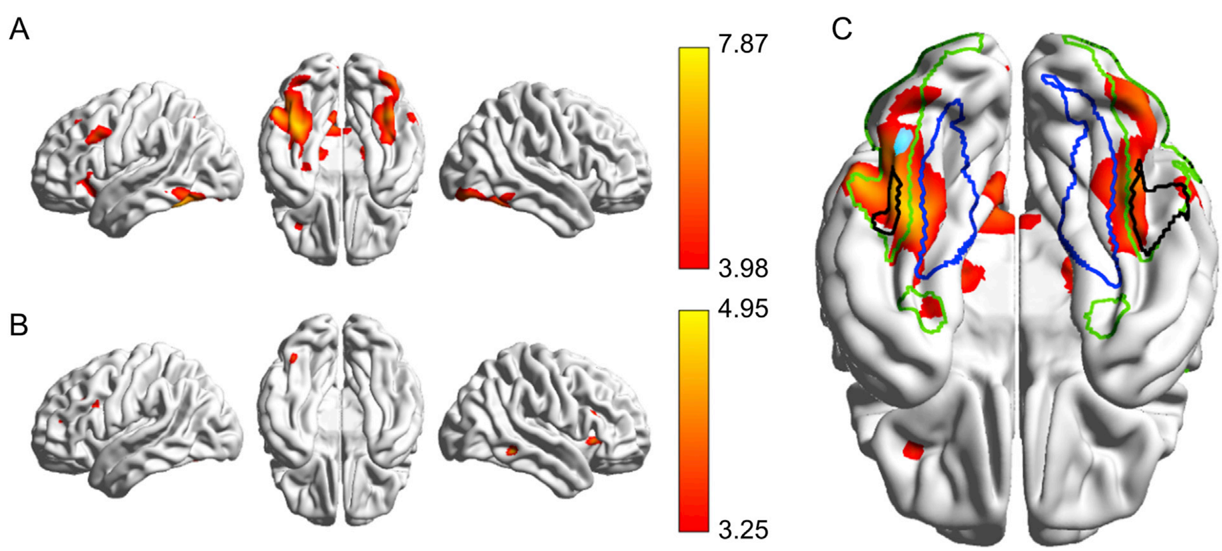

Fig. 6. (A) Left hemisphere, ventral and right hemisphere view of the univariate bird expertise effect: heightened activation for birds in bird experts compared to bird novices (uncorrected threshold of $p < 10^{-4}$, minimum cluster size of 10 voxels). (B) Left hemisphere, ventral and right hemisphere view of the mineral expertise effect: heightened activation for minerals in mineral experts compared to mineral novices (uncorrected threshold of $p < 10^{-3}$, minimum cluster size of 10 voxels). (C) Ventral view of the bird expertise effect (orange – yellow) and the mineral expertise effect (light blue). Dark blue outlines delineate the functional regions with a preference for nonliving objects, green outlines indicate regions selective for living objects and black outlines indicate the bilateral FFA. The figures were created using BrainNet Viewer ((Xia et al., 2013) http://www.nitrc.org/projects/bnv/) and custom Matlab code.

manually delineated in individual participants using functional data from the conditions of faces, living objects, nonliving objects, scrambled and scenes. The expertise effect for birds was tested by comparing the mean activation for the contrast [birds – base] in ornithologists with the mean activation in bird novices (mineralogists and control participants). For each fROI, the results were averaged across the left and right hemisphere.

The results are depicted in Fig. 7A. In all 6 fROIs we found significantly heightened activation for birds in ornithologists compared to bird novices. This included FFA ($N_1 = 19$, $N_2 = 34$, $p < 0.0001$) and the Living region ($N_1 = 20$, $N_2 = 36$, $p < 0.0001$), which are most informative and most responsive to the domain of birds (which are living objects), but also the less responsive regions like pLOC ($N_1 = 20$, $N_2 = 37$, $p = 0.001$),

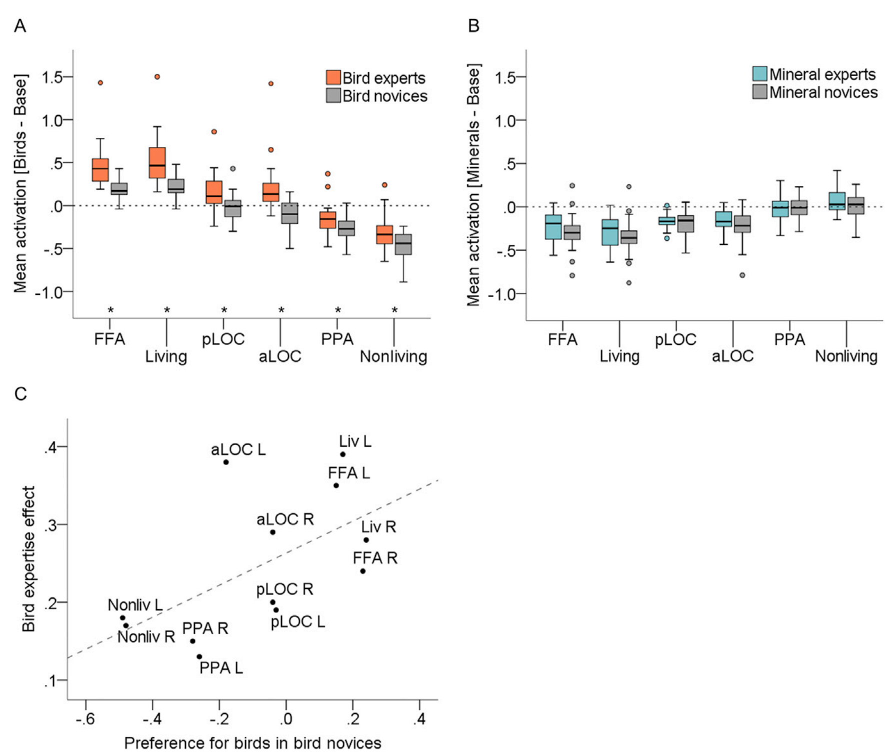

Fig. 7. (A) Mean activation for the [Birds - Base] contrast for bird experts and bird novices (mineralogists and control participants) in 6 functionally defined ROIs (activation was averaged across hemispheres, only subjects with both left and right hemisphere fROIs were included). Boxplots display median and interquartile range, whiskers indicate the minimum and maximum values, dots represent outliers (>1.5 x interquartile range) and significance is indicated by an asterisk. In all 6 fROIs, there was a significant difference between experts and novices. (B) Mean activation for the [Minerals - Base] contrast for mineral experts and mineral novices (ornithologists and control participants). Unpaired t tests revealed no significant differences. In supplementary material (section D, Fig. S3) we have broken down the single difference bars depicted in panels A and B into the constituting two bars (activation for expert condition and activation for base condition separately). (C) Scatterplot displaying a significant positive correlation (Pearson's $r = 0.584$, $p = 0.046$) between the general preference for birds (mean activation for birds in bird novices) and the expertise effect for birds (heightened activation for in bird experts compared to novices) across left (L) and right (R) hemisphere fROIs. The dotted line depicts the linear line of best fit ($y = 0.26 + 0.21x$).

aLOC ($N_1 = 20$, $N_2 = 37$, $p < 0.0001$), PPA ($N_1 = 20$, $N_2 = 37$, $p = 0.005$) and the Nonliving region ($N_1 = 20$, $N_2 = 35$, $p = 0.003$). Nevertheless, we found a significant positive correlation (Pearson's $r = 0.584$, $p = 0.046$) between the fROIs' general sensitivity for birds (average activation for the [birds-base] contrast in bird novices) and the difference in [birds - base]-activation between bird experts and bird novices (Fig. 7C). In other words: the expertise effect for birds was most pronounced in those fROIs that already showed a higher specificity for birds (FFA and Living region). To make sure that the bird expertise effect in the Living region was not driven by the FFA, we excluded FFA voxels from the Living region for each participant and repeated the analysis for all participants for which the bilateral fROIs consisted of more than 20 voxels (Living - FFA left: 42 subjects, average size of 60 voxels; Living - FFA right: 42 subjects, average size of 73 voxels; given that the Living region was restricted to ventral cortex, it is to be expected that voxels responsive to animal bodies would overlap substantially with the FFA, see e.g. Schwarzlose et al. (2005)). Again, we found significantly heightened activation for birds in ornithologists compared to bird novices ($N_1 = 11$, $N_2 = 24$, $p = 0.005$) and the size of the effect was very similar to the effect in the original Living region.

Expertise effects for minerals were measured by comparing activation between mineral experts and mineral novices (ornithologists and control participants) for the contrast [minerals – base]. No effects survived a stringent FWE-corrected threshold. At a lower uncorrected threshold of $p < 0.001$ (with a minimum cluster size of 10 voxels, see Lieberman and Cunningham (2009)), small, distributed effects in left and right prefrontal and ventral temporal regions emerged (Fig. 6B). Here again, the effects were largely the same when comparing mineral experts with the group of control participants in itself.

As illustrated in Fig. 7C, the peak voxel of the cluster of significant activation in left ventral temporal cortex was located more posterior compared to the bird expertise effect in that same region (MNI coordinates of peak voxel (−38, −70, −20)). The absence of effects at an FWE-corrected threshold shows that expertise effects are distributed in a manner that is more convenient for a multi-voxel approach. Nevertheless, the small univariate peaks could still underlie the multi-voxel effects. We performed the same multivariate subject classification analysis as described above in this left ventral temporal cluster, to check whether the effects in this cluster could explain the multivariate results shown above. The resulting decoding accuracy (44.4%) was not significant, meaning that the multi-voxel responses for minerals in this particular cluster did not differ between mineralogists and control participants. This also indicated that the significant subject classification between mineralogists and control participants in the high-level visual aROI (67.4%) was not driven by a very local effect in this left ventral temporal cortex, but signified a more distributed effect across a larger part of high-level visual cortex.

We also performed fROI-based analyses for mineral expertise. The mineral expertise effect was tested by comparing the mean activation for the contrast [minerals – base] in mineralogists with the mean activations in mineral novices. There were no significant differences between these two groups in any of the selected regions (Fig. 7B). This finding further suggests that expertise for minerals induces small and distributed neural effects which are not confined to very specific (known) functional distinctions. Overall, in line with the MVPA findings, the univariate results suggest that the changes in selectivity underlying the MVPA findings are distributed, stronger in ornithologists than in mineralogists, and do not show an obvious overlap in spatial distribution in high-level visual cortex.

Here we restrict the investigation of expertise effects at the level of smaller ROIs to univariate analyses. A priori we decided to only perform the classification and generalization analyses in these three large aROIs because these are the optimal and most sensitive analyses to investigate questions about domain specificity. Post hoc we checked the results in the 6 smaller functional ROIs that were delineated in each participant for the purpose of ROI-based univariate analyses. Overall, the classification performances dropped compared to those in the larger aROIs (e.g. for classifying ornithologists vs. control participants based on the birds condition in the high-level visual cortex: drop from 91.3% to an average of 69.2% across fROIs), in some fROI x condition combinations falling below the statistical threshold. Given the lower sensitivity in these smaller fROIs we refrain from drawing strong conclusions. At best, the results suggest that the higher classification performances in the aROIs do not seem to be based upon one smaller sub-region. We also calculated the correlations between the behavioral scores and the “proportion decoded as expert” in the fROIs. The results confirm most of what we see in the aROIs but with some variability between the fROIs. These results are shown in supplementary material (section B, Fig. S1 and Table S2).

Expertise does not influence the representational similarity of object categories

After having shown that expertise changes the high-level visual multi-voxel activity patterns for objects of expertise in a domain-specific manner, the question emerges whether these changes might be related to a specific altered representation of these objects relative to other object categories. To test this, we applied multivariate correlational analyses to investigate potential differences between the two expert groups and the control participants in the representational similarity between the 7 conditions (faces, birds, living, nonliving, scrambled, minerals, scenes) in high-level visual cortex. Especially the relationship between the expertise condition on the one hand (birds for ornithologists, minerals for mineralogists) and the remaining conditions on the other hand could be informative.

The MDS-plots for the different subject groups can be found in Fig. 8. The mutual relations between the different conditions were strikingly similar across the three subject groups, with a clear distinction between the animate and inanimate categories. The objects of expertise nicely followed this distinction, independently of expertise, and did not seem to suddenly turn up in an unexpected position in their experts. Of course, visual inspection of MDS plots does not substitute statistics, but at least such explorative inspection suggests no obvious effects of expertise which would warrant further statistical testing. More quantitative analyses also did not show any obvious and significant difference between subject groups. We also performed these MVPA-based MDS analyses using data from the low-level visual and frontal aROIs, to again find similar representational spaces in the three subject groups (results not shown).

To sum, expertise does not seem to have a strong influence on the representational similarity between the object category of expertise and other categories. Put bluntly: a mineral is (visually) similar to a rock, even to a mineralogist. (Note that mineralogists will fiercely argue that people should not confuse minerals with rocks.)

Discussion

Conclusions

In the present study, we compared the changes in neural processing that were associated with two very different types of visual expertise: ornithology and mineralogy. Multi-voxel analyses showed that both types of expertise influence neural object representations in high-level visual cortex, while the effects for bird expertise even extended to low-level visual regions and to the frontal lobe, displaying a distributed pattern of expertise effects. Univariate differences in response strength were only found for bird expertise, distributed across all included category-selective regions of interest. Importantly, a multi-voxel generalization analysis indicated that the expertise effects in high-level visual cortex were mostly specific to the domain of expertise. In the frontal lobe, in contrast, changes in object processing due to expertise overlapped significantly across the two different domains of expertise.

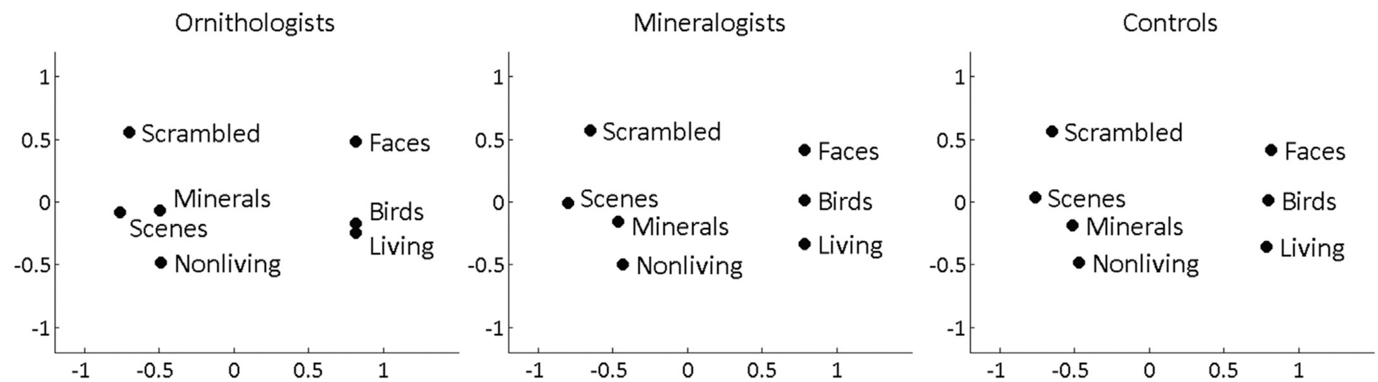

Fig. 8. Multi-dimensional scaling plots depicting the neural similarity between the 7 different object categories for ornithologists, mineralogists and control participants in the high-level visual aROI. The representational similarity between the different conditions is very similar across the three subject groups, with a clear distinction between living and nonliving object categories.

Top-down influences of expertise

In the one-back task that participants performed in the scanner, for both expert groups the ability to detect repetitions of images belonging to the domain of expertise was higher compared to images belonging to the other expert domain, with in addition better performances on a post-scan recognition task. These results are in line with an earlier study which showed that experts had a clear preference for pictures of objects related to their field of expertise (Hershler and Hochstein, 2009). The fact that objects of expertise appear to be more salient to experts may reflect the relevance of top-down attentional control in expertise. Harel et al. (2010) demonstrated that the level of engagement experts show for the objects of expertise affects the neural responses to these expert objects. Based on their findings, we would predict smaller or even no effects of expertise in tasks which do not tap into the expertise.

Frontal cortex would be the most likely source of this top-down attentional control (Corbetta and Shulman, 2002; Harel et al., 2010; Harel, 2015). Our analyses of the frontal lobe provide some insight into the nature of these top-down influences. By applying the multi-voxel generalization analysis, we demonstrated the presence of domain-general effects of expertise in frontal lobe. Several other studies, on various domains of expertise, have shown neural expertise-related changes in frontal lobe as well: e.g. for chess expertise (Krawczyk et al., 2011), radiological expertise (Bilalić et al., 2014), car expertise (Harel et al., 2010) and novel objects trained in the lab (Moore et al., 2006). However, the present study is unique in the sense that we demonstrate for the first time that these expertise effects in frontal lobe are similar across very different types of visual expertise. While our findings point towards the dominance of domain-general processes in frontal cortex, they do not pinpoint the exact processes that are involved. Probably it is a mixture of processes (attentional control, memory, arousal, …).

Informativeness

Expertise effects in high-level visual cortex did not generalize across different domains of expertise, indicating that expertise-related changes in the neural object representations in this region depend on the specific domain of expertise. We also showed that the peak activation (peak voxels of univariate activation) for both types of expertise did not overlap, possibly explaining the lack of generalization in MVPA. Note that the differences in effect size between the stronger bird expertise effects and the weaker mineral expertise effects is not by itself evidence for domain-specific effects of expertise. To the contrary, the situation that the effects in one domain would just be a stronger version of the effects in the other domain is exactly the situation that was simulated to estimate the maximal between-domain generalization possible given the within-domain decoding. Instead, the crucial evidence for domain specificity in high-level visual cortex was the lack of generalization between the two domains of expertise, significantly lower than the estimated maximal generalization.

Strikingly, we found that the expertise-related enhanced activation for birds was most pronounced in those functional regions that already showed a higher sensitivity for birds in bird novices, like the FFA and the Living region. This result is similar to the results in a recent study by Brants et al. (2016), who showed that training to discriminate between novel objects strengthens the responses in a pre-existing specificity map for the to-be-trained objects. It has been suggested that the extent to which neurons and brain regions are involved in a particular type of expertise depends on their informativeness for the domain of expertise and the task at hand (Brants et al., 2016; Op de Beeck, 2012; Op de Beeck and Baker, 2010). This concept of informativeness has its origin in the field of visual neuroscience (Schoups et al., 2001; Raiguel et al., 2006). However, we should note that in the current study, we also showed the presence of bird expertise effects in PPA and the Nonliving region (like other studies before us have found expertise effects in object-selective regions, see introduction), which are considered to be “non-informative” regions. Furthermore, we were not able to show similar effects in informative regions for mineralogists. Thus, informativeness is a partial but not a full explanation of the domain-specific distribution of expertise effects in visual cortex.

Apart from the domain in which subjects have acquired expertise, the type of training with the object category could also influence the neural effects of expertise. In the study by Brants et al. (2016), in which both type of training and expert object category were manipulated across a group of laboratory-trained participants, only object category influenced the reported neural expertise effects. However, some studies have shown differential changes in the neural representations of novel objects depending on the type of training participants received (Wong et al., 2009; Wong et al., 2012). Type of experience is of course very hard to control for when comparing two real-world domains of expertise. The way in which participants in the current study gained experience with birds or minerals could play a role in the resulting neural expertise effects, however, we did not take type of training into account when selecting participants for this study and therefore we cannot make statements on how this might have influenced our results.

This study fits into the bigger framework of ongoing discussions regarding the neural processes that underlie expert object recognition, in which two contrasting views play a major role. The perceptual process view sees expertise as a stimulus-driven, domain-general process, with expertise-related neural changes located in one specific region that encompasses the type of processing necessary for expert object recognition (Gauthier and Tarr, 1997). The expertise hypothesis, a more specific version, focuses on the relation between expertise and face processing. According to this hypothesis, FFA is the brain region in which “expert processing” takes place (Gauthier et al., 2000, 1999). Its selectivity for faces has arisen due to the fact that we are all experts in processing faces, and not because faces are a special category.

The interactive view on expertise on the other hand is domain-oriented and sees expertise as an interaction between bottom-up and top-down factors (Harel et al., 2013). The neural correlates of expertise are not limited to one specific region in the brain but depend upon the domain of expertise and the task demands. In line with this view is the idea of informativeness which was mentioned above. In the current study, expertise effects were found in FFA, as predicted by the expertise hypothesis, but also outside of FFA and even outside the visual cortex. Furthermore, the domain-specific effects that were found in high-level visual cortex point more towards the domain-oriented view on expertise: expertise-related changes in this region were localized differently depending on the domain of expertise.

Limitations and future directions

The present study provides a substantial advance in our understanding of how different domains of expertise change the brain. However, many questions remain. In terms of our own data, it is puzzling that the expertise effects show a strong difference in size between ornithology and mineralogy. The successful subject classification in high-level visual cortex and the significant generalization in frontal lobe show that mineral expertise effects are present, but they are smaller compared to effects of bird expertise. How can we explain this difference in effect sizes? There was a minor difference in the level of expertise between the two subject groups. We indicated that this difference is insufficient to explain the differential effect size at the neural level. A different possibility is that ornithology is a more visual expertise compared to mineralogy. In fact, both domains are only partially visual and also rely on other modalities (e.g., sound for birds and touch for minerals). The relative importance of the different modalities might differ between the domains of expertise. However, according to experts in the field, the shape of a mineral is still a very important determinant for identification and classification.

The results of the subject classification analyses showed a second curious finding. In high-level visual cortex, the interaction between domain of expertise and stimulus condition was as expected: ornithologists could be classified based on their neural response patterns for birds and mineralogists based on the neural responses to minerals. However, in the low-level visual ROI, mineralogists could be distinguished from control participants based on their response patterns for birds. This result was not related to behavior, given that mineralogists and control participants did not show convincing differences in performance on the behavioral tasks for birds. There was also no difference in univariate activation for the [birds - base] contrast between the two subject groups.

Following the major distinction underlying the large-scale organization of neural object representations, we chose to compare one animate and one inanimate domain of expertise. Therefore, differences in neural expertise effects between the two domains of expertise could be related to this animate-inanimate distinction, instead of the two domains in itself. To shed light on this issue, two different animate object categories of expertise should be compared (e.g., Tanaka and Taylor, 1991; Tanaka and Curran, 2001), as well as two inanimate expert object categories. Furthermore, the level of homogeneity of an object category influences discrimination of the objects at the subordinate level (individual objects that are perceptually very similar make discrimination harder, D'Lauro et al., 2008) and subsequently may influence the underlying neural expertise effects. Therefore, the selected expert object categories should also be matched based on their homogeneity. When comparing ornithology with mineralogy, it is possible that the categories of birds and minerals differ in their intra-category homogeneity (note that issues like these can never be completely avoided when comparing two very different real-world domains of expertise).

An important limitation of the present study is that expertise is manifested at the behavioral level in the ability to make fine-grained within-category distinctions (e.g., discriminating among birds), whereas at the neural level we investigated selectivity for between-category distinctions (e.g., discriminating birds from other objects). Important effects might be missed by this lack of specificity at the neural level. Further studies should be done to investigate the neural representation of more subordinate distinctions, although this approach might encounter the limits of multi-voxel analyses in terms of distinguishing fine object distinctions (see e.g. Brants et al. (2016)). Such studies could extend the present findings, which reveal domain-specific effects of expertise on between-category selectivity in high-level visual cortex combined with domain-general effects in the frontal lobe.

Conflicts of interest

None.

Acknowledgements

This work was supported by the European Research Council (Grant ERC-2011-Stg-284101 to H.O.d.B.). The data will be made available on the Open Science Framework (https://osf.io/mpq8e/). We wish to thank Nicky Daniëls for technical assistance.

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.neuroimage.2017.12.013.

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